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CONTACT ORGANS IN THE KILLIFISHES OF WOODS HOLE.¹

H. H. NEWMAN.

In a former paper² the writer had occasion to describe certain interesting structures occurring as a secondary sexual character in the spawning males of four species of Pæciliidæ occurring in the waters about Woods Hole, Mass. These structures were designated "contact organs," the writer venturing to use a new term for the reason that no very similar structure had been previously described. Contact organs seem to have a somewhat similar function to that of the pearl organs of other authors, but in structure they are utterly different.

Although these little organs have been observed on only four species, it seems highly probable that they may prove to be characteristic of the Pæciliidæ, and hence of some systematic importance.

OCCURRENCE.

Contact organs are found on all spawning males of the following four species: *Fundulus heteroclitus*, *F. majalis*, *F. diaphanus* and *Cyprinodon variegatus*.

They occur regularly in the following regions:

1. On the rays of the dorsal and anal fins.
2. On the ventral fins in *Fundulus heteroclitus* and *F. diaphanus*.
3. On the margins of the scales of the sides, cheeks, snout and top of head. In *F. majalis* they also cover the back from the head to the dorsal fin.

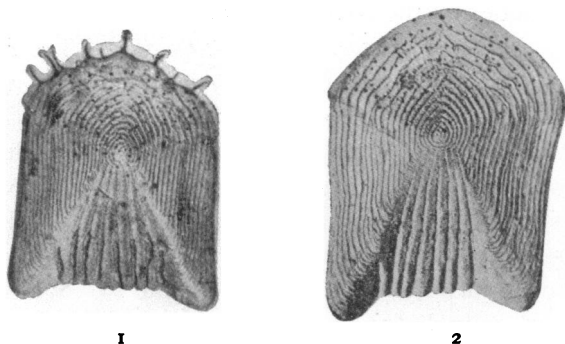
These are the regions in the males that come into most intimate contact with the female during the spawning act proper or during the preliminary courtship. Differences as to the details of the distribution of these organs among the species are closely correlated with differences in the spawning attitude.

In *Fundulus heteroclitus* the spawning takes place in pairs, a

¹ Contributions from the Zoölogical Laboratory, University of Texas, No. 97.

² H. H. Newman, BIOLOGICAL BULLETIN, Vol. XII., No. 5.

female being clasped by only one male at a time. The two bodies are closely pressed together side to side, the tails turned considerably to one side and the heads to the other. The male

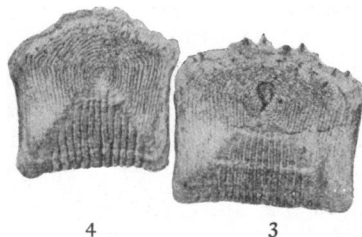


Photographs showing scales with and without contact organs, $\times 12$.

FIG. 1. Scale from the side of a large male *F. majalis*.

FIG. 2. Scale from a corresponding part of the body of a large female *F. majalis*.

clasps the female securely about the body back of the dorsal and anal fins, using as claspers his large, strong dorsal and anal. For additional security the small ventral fins on the sides of contact are locked. On the body the points of closest contact are



Photographs showing scales with and without contact organs, $\times 12$.

FIG. 3. Scale from the lateral line region between the dorsal and anal fins of a spawning male *Cyprinodon variegatus*.

FIG. 4. Scale from a similar location of a spawning female *Cyprinodon variegatus*.

the region of the sides between dorsal and anal fins and the side of the head, which is bent sharply against that of the female. The distribution of the contact organs is in detail just what might be expected on the supposition that the name given them is apt. The organs are largest and most numerous on the proximal parts of the dorsal and anal fin rays and on a rather narrow zone of the body immediately between these two fins. They are fairly

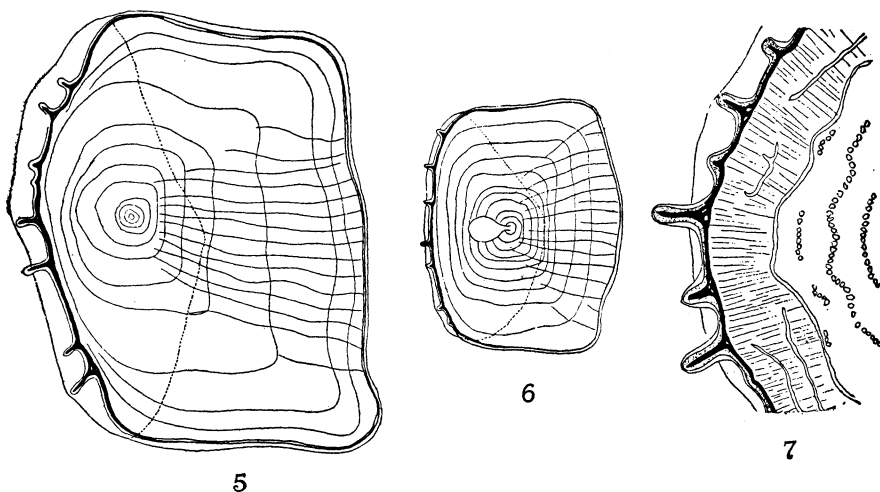
large and numerous on the sides of the head and on the ventral fins, and comparatively small and scattering on the sides anterior and posterior to the point of greatest pressure.

The distribution of the contact organs in *F. diaphanus* is strikingly like that just described for *F. heteroclitus*. The spawning attitude has not been observed, but, from analogy, one might be fairly certain that it closely resembles that of the latter.

F. majalis seldom spawns in captivity and when the former paper was written the writer had never observed a case of spawning in this species. During the following summer, however, several instances of this phenomenon came under observation. *F. majalis* does not seem to spawn in pairs, but two or more males coöperate with a single female. On one instance as many as five males were seen piled in a struggling heap over one female. The whole mass was in strong vibration and the surrounding water was clouded with milt. Although the exact details of the spawning attitude could not be made out on any occasion, it is certain that the points of contact are much less restricted than in *F. heteroclitus*. The nearest males clasp convenient parts of the female and the outer males seemed to clasp the inner ones or to crowd their bodies into the mass backforemost. The distribution of contact organs accords with this rather promiscuous manner of spawning. They are largest and most numerous on dorsal and anal fins and on a zone of the body between these fins. There are none on the ventral fins as they could not be locked in spawning. On the dorsal surface of body and head, on cheeks and snout, they vary in size and abundance, but in many specimens the ventral surface of the body and the ventral and pectoral fins are the only parts not provided with them.

Cyprinodon variegatus, a small species with decidedly compressed body, spawns in pairs in much the same fashion as *F. heteroclitus*, but the short body and very flat sides give a greater area of contact between male and female. Corresponding with this greater area of contact the contact organs are more generally distributed over the body than in any of the other species. On the very high dorsal fin, however, they are restricted to the proximal portion of the rays, for only that portion can touch the sharp-edged back of the female. They occur plentifully on the smaller anal and ventral fins.

In all species the contact organs occur on the top of the head and upon the snout, places where there is little or no direct contact in spawning proper. These regions, however, are used constantly as contact surfaces during courtship and rivalry. During courtship the male swims beneath the female and seems to guide her about from place to place by gently "butting" her with the top or sides of the head. Rivalry in at least two of the species, *F. heteroclitus* and *Cyprinodon variegatus*, is very intense. Two males rush at one another head on and strike one another savagely with cheeks, jaws and snouts. Such contests may be



Camera drawings of typical scales from the region between the dorsal and anal fins of spawning males.

FIG. 5. *Fundulus heteroclitus*, $\times 16$.

FIG. 6. *F. diaphanus*, $\times 16$.

FIG. 7. Enlarged detail drawing of a portion of the exposed margin of a scale taken from the side of a male *F. majalis*. The black region represents the horny margin of the growing region of the scale that is prolonged into spikes that support the contact organs. The stippled area represents the dermis. The clear outside area represents the epidermis. The striated portion in the non-calcified portion of the scale, $\times 30$.

kept up at intervals for days. A number of specimens were examined after they had been engaged in combat for some time to determine the effect of fighting upon the contact organs. In all cases the latter were found to be much worn, many showing the supporting spike stripped of dermis and epidermis. Apart from

this no damage seems to have been suffered. No doubt the violent contact of these organs is somewhat painful to both parties in the struggle, for, judging by their nerve supply, they must be very sensitive.

For diagrams showing the average distribution of contact organs in spawning males of the four species see Text Plate II. of the paper previously referred to.

ARRANGEMENT AND POSITION OF CONTACT ORGANS ON SCALES AND FINS.

On the Scales. — At the height of the spawning season they occupy the entire free edge of the scales on which they occur, standing out like curved fingers at an angle of about thirty degrees from the flat surface of the scale. The scales of the body

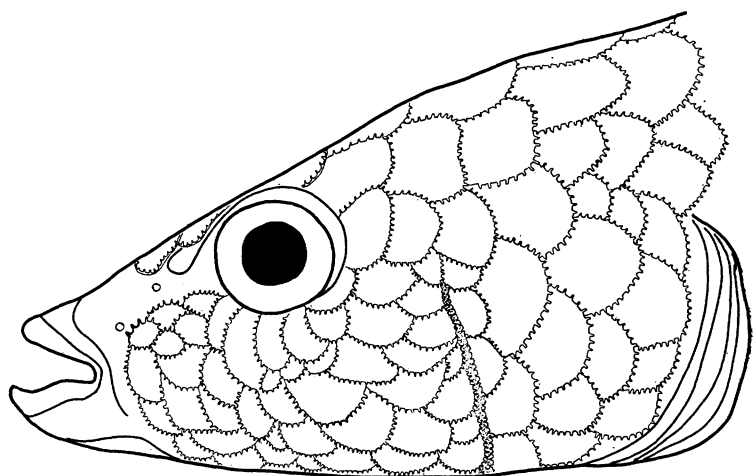


FIG. 8. Camera drawing ($\times 4$) of the head of a male *Fundulus majalis* with complete equipment of contact organs. Notice that the latter occur at fairly regular intervals along all free margins of the scales.

proper have only an arc of their circumference free and hence can produce contact organs only on this free surface (see Figs. 1, 3, 5 and 6). On the head and cheeks, however, many of the scales are plate-like with the whole circumference free. In the latter case contact organs occur around the whole margin. Fig. 8 shows in detail the distribution of the organs on the head of typical male of *F. majalis*, in which the scales show varying amounts of

free margin. The only scales with entirely free margin shown here are certain small ones on the snout. On top of the head, however, there are several large plates with the entire margin free.

On the Fins. — Fig. 9 is a camera drawing showing the distribution of the organs on the anal fin of a large male *F. majalis*. It will be noted that they are largest and most numerous on the ends of the rays of the small ventral lobe, the part most closely pressed against the body of the female in spawning. They occur

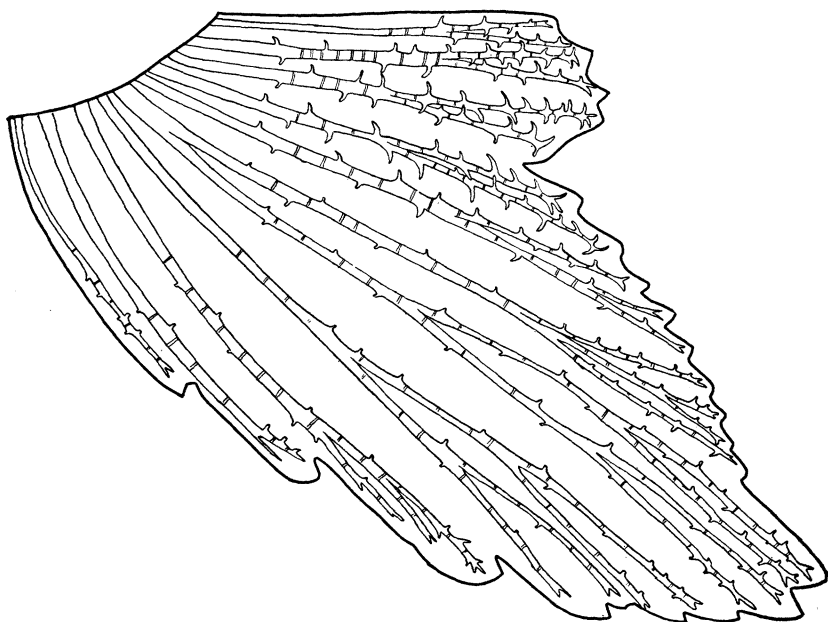


FIG. 9. Camera drawing ($\times 4$) of the ventral fin of a very large male *F. majalis*. The preparation was cleared in strong KOH solution.

as branches from the bony fin rays, usually one or two to the joint, and frequently form clusters at the distal end of the rays where branching is occurring. Fig. 10 shows a condition of this sort on one ray of the fin shown in the previous figure, where it was impossible to show all of the elements in the terminal cluster. The portion represented in solid black is the bony portion. It will be noted also that the majority of the contact organs are slightly hooked toward the base of the fin. This position should

be effective in enabling the male to hold the female more securely. In some specimens of *F. majalis* the organs are restricted to the small posterior lobe. From the few observations made thus far on the spawning attitude of this species it would seem that in many cases the anal fin can play only a minor part in clasping. Hence it may be that there is at present a tendency to reduce the number of organs on this fin. The writer takes occasion to point out this weak spot in the evidence in favor of the general conclusion that the distribution of contact organs is intimately correlated with the spawning attitude. The possible explanation may lie in the fact that only a very few observations have been made of spawning in this species, and the attitudes then seen may depart somewhat from those assumed in the open. All observa-



FIG. 10. Camera drawing ($\times 12$) of the distal portion of a single ray from the posterior lobe of the anal fin of a spawning male *F. majalis*. The solid black represents the osseous structure of fin ray and contact organs, the single line the boundary of the epidermal portions.

tions agree, however, as to the promiscuity of the spawning. In both *F. heteroclitus* and *Cyprinodon variegatus*, in which all of the details of the spawning attitude have been accurately determined, the correlation between spawning attitude and distribution of the contact organs holds without exception. The relationship of the organs to the fin rays is the same, with minor differences, in all species studied.

Structure. — Attempts to section the contact organs were disappointing. After complete decalcification there still remained in the central supporting spikes crystals of some hard substance, probably guanin, that resisted the knife edge and tore through the section. Fragments of tissue from such sections revealed the fact that the epidermal covering was thin and of the usual type and that the dermal layer was much thicker and was composed of rather loosely arranged connective tissue, blood vessels and a few nerve fibers. A substitute method was found, how-

ever, that served to reveal the essential histological structure almost as well as the usual method of sectioning and staining. Scales or fins were soaked for a day or more in rather strong KOH solution. This treatment renders all tissues except the osseous parts quite transparent, so that, by carefully manipulating the illumination, practically all details were revealed under low powers of the microscope.

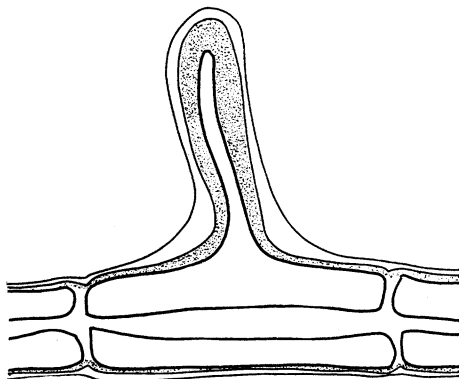


FIG. 11. Camera drawing ($\times 60$) of a single contact organ on a ray of the anal fin of a male *F. majalis*, cleared in KOH solution. The unshaded central portion represents the osseous portion of fin ray and contact organ, showing the continuity of the two. The stippled region is the dermis overlying the osseous portions. The unshaded marginal portion represents the epidermis.

On the scales (see Fig. 7) the spike-like core is continuous with the newest layer of osseous material, while on the fins (see Fig. 11) the core is of a piece with the outer layer of the fin rays. In other respects the organs are alike in both locations. Surrounding the core which is dense and hard, although somewhat elastic, is a thick layer of dermis, more abundant near the tip of the organ. The comparatively thin epidermis seemed to be stretched over the tip of the organ and was frequently broken. Near the base, however, it was as thick or thicker than the dermis of that region. The difference between these structures and pearl organs may be seen at once in the comparatively secondary importance of the epidermis and in the core of dermis with its osseous support. The pearl organ is merely an epidermal callosity.

ORIGIN, DEVELOPMENT AND DISAPPEARANCE.

In order to determine how early in the season the contact organs begin to make their appearance, a number of specimens of the two species most accessible, *F. heteroclitus* and *F. majalis*, were very kindly collected for me by Mr. G. M. Gray, of the Woods Hole supply department. The results of the examination of these specimens are shown in the following tables :

TABLE I.

(*F. heteroclitus* males, collected April 27, 1907.)

No. of Specimens.	Distribution of Contact Organs.
5	A few on the posterior lobe of the anal fin.
3	Fairly numerous on the tips of nearly all of the rays of the anal fin.
1	Plentiful on the rays of the posterior lobe of the anal fin.
1	Scattering distribution over nearly the whole area of the anal fin.
1	Numerous on all of the rays of the posterior two thirds of the anal fin.
8	None.

According to these data the earliest appearance of contact organs in this species is on the anal fin, especially on the posterior lobe of the latter. They appear first upon the distal ends of the rays and from there extend gradually toward the base. One is tempted to suggest a correlation between the early appearance and the functional importance of these organs. There seems to be no doubt that the anal fin is of prime importance in claspings.

TABLE II.

(*F. heteroclitus* males, collected May 14, 1907.)

No. of Specimens.	Distribution of Contact Organs.
3	On anal fin only.
2	On anal fins and on the scales of the body zone between the dorsal and anal fins.
5	None.

Specimens taken in large numbers about two weeks later nearly all showed the full equipment of contact organs. The development, therefore, is a very rapid one, taking place largely within a fortnight.

The conditions in the other species (*F. majalis*) were somewhat different. Specimens collected April 27, 1907, showed no contact organs. Those collected on May 14 of the same year showed conditions tabulated as follows :

TABLE III.

(*F. majalis* males collected May 14, 1907.)

No. of Specimens.	Distribution of Contact Organs.
2	Fairly numerous on the cheeks.
4	On cheeks, top of head, and around eyes.
5	On cheeks, top of head, around eyes, and a few rudiments on the body zone between dorsal and anal fins.
1	Rudiments on cheeks and around the eyes, a few on the tips of the anterior rays of the dorsal fin.
1	Fairly numerous on cheeks and around the eyes, scattering on top of head, a few on the dorsal fin, and numerous on the body zone between the dorsal and anal fin.
1	Numerous on cheeks and around the eyes, scattering on top of the head, numerous on body zone between the dorsal and anal fins, and on the distal portions of nearly all of the rays of the dorsal fin, and a few on the posterior lobe of the anal fin near the tips of the rays.

The order of appearance of the organs in the various regions seems to be about as follows: (1) On cheeks and around the eyes, (2) on top of head, (3) on the body zone between the dorsal and anal fin, (4) on the dorsal fin, (5) on the anal fin.

Any attempt to correlate this order of appearance with the relative functional importance of the organs in the different regions meets at once with serious difficulties. It can hardly be supposed that the organs in the head region are of more importance as spawning accessories than are those on the dorsal fin. The fact, however, that the organs on the head are used in the preliminary phases of spawning, such as courtship and rivalry, might better account for their early appearance. Thus the factor of priority of functioning might be conceived of as outweighing functional importance. In *F. heteroclitus*, however, the opposite condition seems to prevail. The difference may lie in the fact that, in *F. heteroclitus* the importance of the fins as claspers is much more pronounced than in *F. majalis*.

The order of appearance of the individual contact organs on the fin rays has been referred to. They appear first on the distal portion of each ray, but, as the ray increases in length, those first formed are separated farther and farther from the tip of the ray. Later they appear proximal to those that were first formed.

On the scales the first organ to appear is always located in the center of the exposed arc of the scale. Many specimens of both

species taken in April and in May showed, in certain regions, but one contact organ to the scale. From the center they are produced outward in both directions. A common condition observed in specimens of *F. heteroclitus* taken in May was that of one rather large organ in the middle of the free edge, flanked on each side of the center by a small organ. There is abundant evidence that other organs may later be intercalated between those first formed.

The contact organs disappear for the season in about six to eight weeks after the close of the spawning season. Specimens collected early in September showed only the faintest traces of the organs. Evidently, judging by appearances of these vestiges, they are partly worn off by friction and partly resorbed. They leave a permanent record of themselves in the angularly wavy outline of the newest osseous ring of the scales. No such trace seems to be left on the fin rays.

Function. — Two possible functions might be subserved by the contact organs, that of frictional surface on the parts of the body of the male with which he holds the female in spawning, and that of contact sensation. That the former function is well subserved is evidenced by the roughness that one notes with the fingers wherever the contact organs are well developed and numerous, and by the fact that the male is actually able to hold the female quite firmly for several seconds. The fighting males are able to inflict any real injury upon one another by means of the contact organs is highly improbable, although they strike one another fiercely with parts well armed with the latter. That scales and fins are decidedly sensitive to contact is well known. Microscopic examination of these parts, prepared by special neurological methods, failed to show that the contact organs were any more richly enervated than the rest of the free edge of the scale or the general surface of the fin. It is probably true, however, that the projecting position of the contact organs renders them more subject to contact sensation than the surrounding flat regions of scales and fins.